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STOMACH CONTENTS OF PORPOISE, *STENELLA* SPP., AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, IN MIXED-SPECIES AGGREGATIONS

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ABSTRACT

Haul-by-haul analysis of stomach contents of spotted porpoise (*Stenella attenuata*), spinner porpoise (*S. longirostris*), and yellowfin tuna (*Thunnus albacares*) from six net hauls made on mixed-species aggregations in 1968 indicates that an ommastrephid squid (probably *Dosidicus gigas*) was the most important food item in terms of co-occurrences in the three species and in terms of the volume and number. The ommastrephid occurred in significant numbers and/or volume in each haul in all the species examined, albeit to a lesser degree in the spinner porpoise than in the other two species. Overlap of elements in the stomach contents was greatest between the tuna and the spotted porpoise. In addition to the ommastrephid, the small scombrid *Auxis* sp. and epipelagic exocoetids such as *Oxyporhamphus micropterus* were important to both. The portunid crab *Euphylax dovii* was very important in the tuna but absent in both species of porpoise. Onychoteuthid and enoploteuthid squids were important in some hauls in both species of porpoise but were all but absent from the tuna. Small mesopelagic fishes, mainly myctophids and gonostomatids, were important in the spinner porpoise, but not in the spotted porpoise or the tuna. Relative frequencies of empty stomachs and state of digestion of stomach contents indicated that the spinner porpoise does not feed at the same time as the spotted porpoise and tuna. In spite of overlap among the three species in nearly all of the food components, these results suggest that the tuna and spotted porpoise feed together largely on epipelagic prey, whereas the spinner porpoise for the most part feeds deeper and at different times of day; furthermore, only the tuna eats crustaceans.

Small pelagic delphinids (*Stenella attenuata, S. longirostris,* and *Delphinus delphis*) in the eastern tropical Pacific are commonly encountered with yellowfin tuna (*Thunnus albacares*) in large mixed-species aggregations. The association between the fish and the cetaceans is very tight (Perrin, 1969, 1970). Although the reason for the association is unknown, the possibility that it is food-based immediately suggests itself. Alverson (1963) examined the stomach contents of 2,846 yellowfin tuna from the eastern tropical Pacific and found the major components to be fish (46.9% of total volume) and crustaceans (45.4%). Cephalopods accounted for only 7.6% of the volume. He encountered a wide variety of food items and changes in species composition from area to area. He therefore concluded that yellowfin tuna are nonselective feeders, foraging on whatever pelagic or benthic organisms of suitable size are locally available. Fitch and Brownell (1968) reported on fish identified from otoliths taken from spotted porpoise, *Stenella graffmani* (= *attenuata*)[4] and spinner porpoise (*S. longirostris*) caught in

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[4] The taxonomy of the spotted porpoises is confused. Recent morphological studies (Perrin, 1972) have shown that the spotted porpoise in the eastern Pacific is conspecific with the spotted porpoise that occurs around Hawaii. Accordingly, the name *S. attenuata* (Gray, 1846), which was applied by True (1906) to the Hawaiian form, is used here for the eastern Pacific form. This name has priority by date over *S. graffmani* (Lönnberg, 1934). This usage is provisional, pending the outcome of current studies comparing forms in the Atlantic and Pacific. *S. attenuata* may be a junior synonym of *S. frontalis* (Cuvier, 1829), which was described from the tropical North Atlantic.

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TABLE 1.—Collection data for stomach contents examined from yellowfin tuna, spotted porpoise, and spinner porpoise from the eastern tropical Pacific.

Net haul	Date (1968)	Location (lat., long.)	Time of day (h)	Yellowfin tuna captured (t)	Estimated composition of porpoise school: *Stenella attenuata* (No.)	Estimated composition of porpoise school: *Stenella longirostris* (No.)	Stomachs examined: *Thunnus albacares* (No.)	Stomachs examined: *S. attenuata* In field (No.)	Stomachs examined: *S. attenuata* In lab (No.)	Stomachs examined: *S. longirostris* In field (No.)	Stomachs examined: *S. longirostris* In lab (No.)
1	9 April	12°51'N, 93°18'W	1045	6	350	150			32		4
2	12 April	7°11'N, 90°32'W	1245	35	1,300	200	14		25	18	5
3	15 April	7°28'N, 91°15'W	1345	45	300		20	20			
4	16 April	7°30'N, 92°06'W	0800	60	1,500		21	24			
5	17 April	7°50'N, 92°32'W	1100	50	600		19	20		19	
6	18 April	7°58'N, 92°56'W	1130	35	350	50	5	19			
Total							79	83	57	37	9

association with tuna in the eastern tropical Pacific. On the basis of knowledge about the depth distributions of the species encountered, they concluded that the spotted porpoise had been feeding within 30 m of the surface and the spinner porpoise had been feeding to 250 m or more beneath the surface. Squid remains were present in some of the stomachs examined by Fitch and Brownell but were not included in their analysis.

In view of the nonselective feeding habits of the yellowfin tuna, analysis of comparative feeding habits of tuna and porpoise in mixed aggregations must be based on stomach contents collected from two or more of the species taken together in net hauls.

In this paper we report the results of the examination of stomach contents of 79 tuna, 140 spotted porpoise, and 46 spinner porpoise, taken in seine hauls on yellowfin tuna in 1968.

MATERIALS AND METHODS

The animals examined were captured in six net hauls by a tuna seiner (Table 1). The tuna were marked with numbered dart-type spaghetti tags and placed in the vessel's refrigerated fish holds. Stomachs were subsequently collected from the marked fish and preserved entire in 10% Formalin[5] when the catch was unloaded and prepared for processing ashore. Most of the porpoise stomachs were examined in the field and only selected items of the contents preserved in 10% Formalin for later identification (Table 1). The remainder of the stomachs were from animals frozen entire and later dissected ashore. Only the contents of the forestomach (oesophageal stomach) were examined.

The tuna taken during the cruise were nearly all about 1 m long. A random sample of 50 fish ranged from 846 to 1,164 mm fork length (average 1,079 mm).

The entire contents of stomachs opened in the laboratory were rough-sorted into fish, squid, and crustacean components. Each food item was identified to the lowest possible taxon,

[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and the volume was then measured. Whole undigested fish were identified by comparison of external characters with published keys or with identified museum specimens and species descriptions. Usually though, digestion had precluded such a procedure, so the remains were dissected and skeletal features were compared with a large series of radiographs of determined specimens from the collections of Scripps Institution of Oceanography, Fish otoliths extracted from the frozen porpoise stomachs allowed identification of completely and nearly completely digested fish. Because the tuna stomachs were initially preserved in unbuffered Formalin, it was not possible to use otoliths from those stomachs because diagnostic otolith features dissolve rapidly in an acidic solution. Some relatively intact squids (*Dosidicus gigas, Symplectoteuthis oualaniensis, Abraliopsis affinis*, and *Onykia* sp.) were found and identified in the stomach contents. Beaks from these specimens and from squids taken on the fishing grounds by dipnetting under lights at night were used to identify isolated beaks and beaks associated with otherwise unidentifiable fragments. Published and unpublished keys to cephalopod beaks and beaks from identified squids in the reference collection of the Marine Mammal Division, Northwest Fisheries Center, were also used in the identifications. Beaks from the ommastrephid squids were relatively easy to identify and separate from those of squids of other families. Although a few of the ommastrephids in the stomachs were identifiable to species, the data for the Ommastrephidae in the tables below are subdivided into only three categories: *ommastrephid A* (probably *Dosidicus gigas*), which includes positively identified *D. gigas* and those fragments (with associated beaks) and isolated beaks most probably belonging to that species on the basis of intrafamilial differences in size and darkening of the beaks; *ommastrephid B* (probably *Symplectoteuthis* sp.), which includes positively identified *S. oualaniensis* and those fragments and beaks most probably belonging to that species or another species of *Symplectoteuthis;* and *unidentified ommastrephid,* which includes those fragments and beaks identified only as from ommastrephids. The larger of the two counts of upper and lower beaks was interpreted as the minimum number of individuals represented. The only crustacean identified, *Euphylax dovii,* was present as readily identifiable nearly complete individuals or intact chelipeds. Because many of the porpoise stomachs contained both the remains (otoliths) of very small fish (myctophids, gonostomatids) and of squid, both of which eat small fish and squid, some of the fish and squid identified were almost certainly present only secondarily. The material was analyzed on a haul-by-haul basis, and the data for each haul are presented and discussed separately. Some effect of the nonselective feeding of tuna, the patchy distribution of prey items, may still be present, however. Since the material analyzed includes some stomachs that were full of relatively undigested food and some that contained only squid beaks and/or otoliths from well-digested meals, it is likely that more than one feeding may be represented in the data for some single-net hauls.

The presentation and analyses of the data are patterned after those in the paper by Pinkas, Oliphant, and Iverson (1971), in which both cephalopod beaks and otoliths were used to identify stomach contents of tunas. The analyses are in terms of volume (for the stomachs examined ashore only), numbers, and percent occurrence. Each of these methods distorts the picture in some way. In the numbers and percent occurrence analyses, unimportant small but numerous organisms may be disproportionately evident. The volume analyses are distorting because the various organisms are digested at different rates and because, as mentioned above, some of the contents were freshly ingested while others were only the remnants of well-digested meals. Otoliths and squid beaks tend to be retained in the gut. An ideal method would involve extrapolating an estimate of the original volume of each prey item and calculating caloric content, but these approaches were beyond the scope of the project. The above caveats notwithstanding, the data do yield considerable information on the relative feeding habits of the three species in mixed aggregations.

The stomachs are considered in three categories: full, with traces, and empty. Full stomachs are defined as those containing fleshy re-

TABLE 2.—Stomach contents of spotted and spinner porpoise taken in a single net haul in the eastern tropical Pacific: Haul 1.

Food item	Spotted porpoise, *Stenella attenuata*, 32 stomachs (22 full, 7 with traces, 3 empty)						Spinner porpoise *S. longirostris*, 4 stomachs (all full)					
	Volume		Number		Occurrence		Volume		Number		Occurrence	
	ml	% of total	No.	% of total	No.	% (n = 29)	ml	% of total	total	% of total	No.	% (n = 4)
Total	7,619	100.0	6,101+	100.0	—	—	447	100.0	5,495	100.0	—	—
Fish	246	3.2	272+	4.5+	22	75.9	196	43.9	5,248	95.5	4	100.0
Exocoetidae	202	2.7	43	0.7	15	51.7	0	—	0	—	0	—
Oxyporhamphus micropterus	195	2.6	41	0.7	13	44.8	0	—	0	—	0	—
Exocoetus	7	<0.1	2	<0.1	2	6.9	0	—	0	—	0	—
Myctophidae	32	0.4	204	3.4	18	62.1	196 ml, not identified to species		3,868	70.4	4	100.0
Diogenichthys sp.	tr.	—	2	<0.1	2	6.9			3,374	61.4	4	100.0
Lampanyctus parvicauda	30	0.4	116	1.9	16	55.2			307	5.6	4	100.0
Lampanyctus idostigma	0	—	0	—	0	—			73	1.1	3	75.0
Benthosema panamense	0	—	0	—	0	—			24	0.4	4	100.0
Myctophum aurolaternatum	tr.	—	6	0.1	5	17.2			25	0.5	3	75.0
Hygophum sp.	0	—	0	—	0	—			5	0.1	4	100.0
Symbolophorus sp.	0	—	0	—	0	—			2	<0.1	1	25.0
Unid. myctophids	2	<0.1	80	1.3	13	44.8			58	1.1	3	75.0
Gonostomatidae: *Vinciguerria* sp.	tr.	—	1	<0.1	1	3.5			98	1.8	3	75.0
Bregmacerotidae: *Bregmaceros* sp.	tr.	—	2	<0.1	2	6.9			842	15.3	4	100.0
Melamphaidae	tr.	—	1	<0.1		3.5			424	7.7	2	50.0
Scopelogadus bispinosus	tr.	—	1	<0.1		3.5			413	7.5	2	50.0
Melamphaes sp.	0	—	0	—	0	—			11	0.2	1	25.0
Stromateidae	tr.	—	8	0.1	5	17.2			0	—	0	—
Cubiceps carinatus	tr.	—	3	<0.1	3	10.3			0	—	0	—
Cubiceps sp.	tr.	—	5	0.1	4	13.8			0	—	0	—
Bathylagidae: *Bathylagus* sp.	0	—	0	—	0	—			11	0.2	1	25.0
Scopelarchidae: Unid. scopelarchid	0	—	0	—	0	—			5	0.1	1	25.0
Unid. fish	12	0.2	13+	0.2+	10	34.5	0	—	0	—	0	—
Cephalopods	7,373	96.7	5,820	95.3	29	100.0	245	54.7	247	4.5	4	100.0
Onychoteuthidae: *Onykia* sp.	358	—	3,386	55.5	27	96.6	59	13.1	26	0.5	3	75.0
Ommastrephidae	157	—	1,569	25.8	29	100.0	47	10.4	68	1.2	3	75.0
Ommastrephid A (probably *Dosidicus gigas*)	127	—	1,108	18.2	29	100.0	47	10.4	45	0.8	3	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	17	—	216	3.5	27	93.1	0	—	0	—	0	—
Unid. ommastrephid	10	—	257	4.4	12	41.4	tr.	—	23	0.4	1	25.0

Enoploteuthidae: *Abraliopsis affinis*	3	—	672	11.0	29	100.0	69	15.3	151	2.7	4	100.0
Histioteuthidae:												
Unid. histioteuthid	tr.	—	1	0.1	1	3.5	0	—	0	—	0	—
Chiroteuthidae:												
Unid. chiroteuthid	tr.	—	3	0.1	1	3.5	0	—	2	0.1	1	25.0
Cranchiidae	tr.	—	3	0.1	2	6.9	0	—	0	—	0	—
Unid. cranchiid	tr.	—	3	0.1	2	6.9	0	—	0	—	0	—
Octopoteuthidae: *Octopoteuthis* sp.	tr.	—	1	<0.1	1	3.5	0	—	0	—	0	—
Unid. cephalopod fragments[1]	[1]6,855	—	—	—	29	100.0	70	15.5	—	—	1	25.0
Unid. cephalopod beaks	3	—	174	2.9	18	62.1	0	—	0	—	0	—
Crustaceans	2	—	2	0.1	2	6.9	6	1.3	—	—	1	25.0
Unid. isopod	2	—	2	0.1	2	6.9	0	—	0	—	0	—
Unid. gammarid amphipods	0	—	0	—	0	—	6	1.3	—	—	1	25.0

[1] Includes bulk of fragments of specimens identified from beaks.

mains; stomachs with traces are those containing only squid beaks and fish otoliths and/or skeletal fragments. The volumetric analyses are based on the full stomachs only. The number and occurrence analyses are based on the full stomachs and those with traces. In addition to the material collected from simultaneous catches of two or more of the three predator species, fish otoliths were examined from another 5 spotted porpoise and 14 spinner porpoise captured with yellowfin tuna in various locations in the eastern tropical Pacific (Appendix Tables 1 and 2).

RESULTS

Haul 1

Only the two species of porpoise were sampled in Haul 1 (Table 2). The results for the species are sharply divergent. For the spotted porpoise, cephalopods predominated in volume, numbers, and occurrence. Onychoteuthid, ommastrephid, and enoploteuthid squids were the major food items. Fish made up an insignificant proportion of the volume and consisted primarily of the epipelagic *Oxyporhamphus micropterus*. In the four spinner porpoise examined, squid and fish were present in all the stomachs, each accounting for about half the total volume. The species composition of the squid component of spinner stomachs was different from that in the spotted porpoise mainly in that one of the unidentified ommastrephids (type B, probably *Symplectoteuthis* sp.) was completely absent, whereas it was present in 27 of the 29 spotted porpoise. Fish, primarily myctophids, predominated in numbers, the ratio of fish to squid being almost precisely the reverse of that for the spotted porpoise. Five myctophid species were present in all four stomachs. By far the commonest fish was *Diogenichthys* sp. (probably *laternatus*). A bregmacerotid, *Bregmaceros* sp., was also found in all four stomachs and was the next most common fish, followed closely by the melamphaid *Scopelogadus bispinosus* and the myctophid *Lampanyctus parvicauda*.

Haul 2

All three species were examined in Haul 2 (Table 3). The results for the spotted porpoise

TABLE 3.—Stomach contents of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single net haul: Haul 2.

Food item	Yellowfin tuna, *Thunnus albacares*, 14 stomachs (12 full, 1 with trace, 1 empty)						Spotted porpoise, *Stenella attenuata*, 25 stomachs (14 full, 8 with traces, 3 empty)						Spinner porpoise, *S. longirostris*, 23 stomachs (5 full, 3 with traces, 15 empty)					
	Volume		Number		Occurrence		Volume		Number		Occurrence		Volume		Number		Occurrence	
	ml	%	No.	% (n = 13)	No.	% (n = 13)	ml	%	No.	%	No.	% (n = 22)	ml (n = 2 full	%	No.	%[1]	No.	%[1]
Total	1,591	100.0	177+	100.0	—	—	762	100.0	1,787	100.0	—	—	1	100.0	439	—	—	—
Fish	844	53.1	34+	19.2	12	92.3	140	18.4	154	8.6	10	45.5		1.8	420	100.0 95.7	2	100.0
Exocoetidae	525	33.0	26	14.7	10	76.9	25	3.3	127	7.1	7	31.8	0	—	0	—	0	—
Oxyporhamphus micropterus	425	26.7	21	11.9	10	76.9	25	3.3	90	5.0	4	18.2	0	—				
Cypselurus sp.	91	5.7	4	2.3	1	7.7	0	—	0	—	0	—	0	—				
Unid. exocoetid	9	0.6	1	0.6	1	7.7	tr.	—	36	2.0	5	22.7	0	—				
Scombridae: *Auxis* sp.	137	8.6	1	0.6	1	7.7	110	14.4	1	0.1	1	4.6	0	—	0	—	0	—
Myctophidae	0	—	Contents preserved in Formalin; not examined for otoliths				tr.	—	17	1.0	6	27.3	tr.	—	321	73.1	2	100.0
Diogenichthys sp.							tr.	—	3	0.2	3	13.6			37	8.4	2	100.0
Lampanyctus parvicauda							tr.	—	1	0.1	1	4.6			1	0.2	1	50.0
Lampanyctus idostigma							0	—	0	—	0	—			7	1.6	2	100.0
Benthosema panamense							0	—	0	—	0	—			257	58.5	2	100.0
Myctophum aurolaternatum							0	—	0	—	0	—			2	0.5	1	50.0
Myctophum sp.							0	—	0	—	0	—			2	0.5	1	50.0
Symbolophorus sp.							tr.	—	1	0.1	1	4.6			3	0.7	2	100.0
Diaphus sp.							0	—	0	—	0	—			2	0.5	1	50.0
Unid. myctophids							tr.	—	12	0.7	4	18.2			10	2.3	2	100.0
Gonostomatidae: *Vinciguerria* sp.							0	—	0	—	0				94	21.4	2	100.0
Bregmacerotidae: *Bregmaceros* sp.							tr.	—	1	0.1	1	4.6			0	—	0	—
Melamphaidae: *Scopelogadus bispinosus*							tr.	—	1	0.1	1	4.6			0	—	0	—
Stromateidae: Unid. stromateoid							0	—	0	—	0	—			2	0.5	1	50.0
Paralepididae: Unid. paralepidid							0	—	0	—	0	—			1	0.2	1	50.0
Unid. fish	182	11.4	7+	4.0	5	38.5	5	0.7	7	0.4	7	31.8			2	0.5	2	100.0
Cephalopods	363	22.8	131	74.0	13	100.0	622	81.6	1,633	91.4	22	100.0	54	98.2	19	4.3	6	75.0
Onychoteuthidae: *Onykia* sp.	0	—	0	—	0	—	9	1.2	28	1.6	10	45.5	tr.	—	1	0.2	1	12.5

Ommastrephidae	105	6.6	89	50.3	11	84.6	114	15.0	1,476	82.6	22	100.0	54	—	14	3.2	6	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	103	6.5	74	41.8	10	76.9	74	9.7	1,220	68.3	22	100.0	54	—	14	3.2	6	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.	2	0.1	15	8.5	8	61.5	40	5.3	262	14.7	20	90.9	0	—	0	—	0	—
Unid. ommastrephid	0	—	0	—	0	—	tr.	—	6	0.3	1	4.6	0	—	0	—	0	—
Enoploteuthidae:																		
Abraliopsis affinis	0	—	0	—	0	—	1	0.1	109	6.1	16	72.7	tr.	—	1	0.2	1	12.5
Histioteuthidae:																		
Histioteuthis sp.	tr.	—	1	0.6	1	7.7	0	—	0	—	0	—	0	—	0	—	0	—
Unid. octopod	0	—	0	—	0	—	tr.	—	1	0.1	1	4.6	0	—	0	—	0	—
Unid. cephalopod fragments[2]	258	16.2	—	—	5	38.5	498	65.4	—	—	11	50.0	0	—	—	—	0	—
Unid. cephalopod beaks	tr.	—	41	23.2	5	38.5	tr.	—	10	0.6	2	9.1	tr.	—	3	0.7	1	12.5
Crustaceans:																		
Portunidae:																		
Euphylax dovii	373	23.4	12	6.8	7	53.9	0	—	0	—	0	—	0	—	0	—	0	—
Unid. material	11	0.7	—	—	1	7.7	0	—	0	—	0	—	0	—	0	—	0	—

[1] Only two stomachs were examined for otoliths; therefore the sample size for fish numbers and occurrence is two, while that for the cephalopods is eight.
[2] Includes bulk of fragments of specimens identified from beaks.

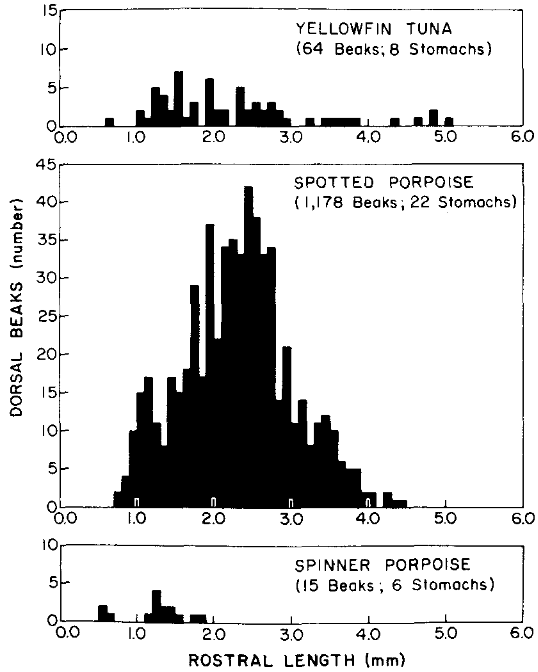

FIGURE 1.—Length frequency distributions of rostral lengths of beaks of ommastrephid squids (type A, probably *Dosidicus gigas*) from stomachs of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single-net haul (Haul 2) in the eastern tropical Pacific.

were much the same as for Haul 1, especially in that cephalopods strongly dominated in both volume and numbers. In this haul, however, ommastrephids rather than onychoteuthids predominated. Though scanty, the numerical results for the spinner were also similar to those for Haul 1. The relative squid volume was disproportionately large because the fish were represented only by otoliths. The contents of the tuna showed most overlap with those of the spotted porpoise. A scombrid, *Auxis* sp., was present in both. Cephalopods and epipelagic fish were important in both. This overlap, however, was overshadowed by some striking differences. The portunid crab *Euphylax dovii* occurred in half the tuna stomachs and accounted for a fourth of the total volume but was absent from the porpoise stomachs (both species). *Onykia* and enoploteuthid squids each occurred in about half the spotted porpoise stomachs but were absent in the tuna.

TABLE 4.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 3.

	Yellowfin tuna, *Thunnus albacares*, 20 stomachs (13 full, 3 with traces, 4 empty)						Spotted Porpoise, *Stenella attenuata*, 20 stomachs (none full, 19 with trace, 1 empty)			
	Volume		Number		Occurrence		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	No.	%	No.	%
Total	837	100.0	112	100.0	16	100.0	75	100.0	—	100.0
Fish	379	45.3	12	10.7	6	37.5	0	—	0	—
Exocoetidae	20	2.4	3	2.7	3	18.8				
Exocoetus volitans	18	2.2	1	0.9	1	6.3				
Unid. exocoetid	2	0.2	2	1.8	2	12.5				
Scombridae: *Auxis* sp.	320	38.2	4	3.6	1	6.3				
Unid. fish	39	4.7	2	1.8	2	12.5				
Cephalopods	3	0.4	78	69.6	8	50.0	[1]75	100.0	19	100.0
Ommastrephidae	2	0.2	68	60.7	8	50.0	66	88.0	2	100.0
Ommastrephid A (probably *Dosidicus gigas*)	2	0.2	53	47.3	8	50.0	32	42.7	2	100.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	tr.	—	16	14.3	6	37.5	34	45.3	2	100.0
Enoploteuthidae: *Abraliopsis affinis*	0	—	0	—	0	—	9	12.0	2	100.0
Unid. Octopod	tr.	—	9	8.0	1	6.3	0	—	0	—
Unid. Cephalopod fragments	1	0.1	—	—	5	31.3	—	—	1	50.0
Unid. Cephalopod beaks	tr.	—	1	0.9	1	6.3	—	—	1	50.0
Crustaceans: Portunidae: *Euphylax dovii*	455	54.4	22	19.6	10	62.5	0	—	0	—

[1] Specimens were preserved from two stomachs only; therefore the sample size for the cephalopod taxa is two.

A striking difference between the data for tuna and spotted porpoise on one hand and the spinner porpoise on the other involved the relative number of empty stomachs encountered. Only 1 tuna stomach of 14 and 3 spotted porpoise stomachs of 25 were empty, whereas 15 spinner porpoise stomachs of 23 contained no food remains. The chance of this difference occurring by chance due to sampling error, based on chi-square analysis and assuming commonality of tuna and spotted porpoise, is less than 0.001, indicating that in the aggregation fewer spinner porpoise than spotted porpoise and tuna had been recently feeding or that the spinner porpoise had regurgitated their stomach contents during the fishing operation.

The spinner porpoise had eaten smaller squid than had the spotted porpoise and tuna. Clarke (1962) demonstrated that beak size within a species is closely correlated with total body weight. The sample of beaks of ommastrephid A (probably *Dosidicus gigas*) collected from the spinner porpoise clearly belong to a different size distribution than those taken from the spotted porpoise and the tuna (Figure 1), indicating that the spinner porpoise on the average had been feeding on smaller squid.

Haul 3

Only yellowfin tuna and spotted porpoise were examined in Haul 3 (Table 4). The porpoise stomachs were all nearly empty, containing only hard parts of squid. Except for the complete absence of fish in the porpoise stomachs, the results for the two species were similar

TABLE 5.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 4.

Food item	Yellowfin tuna, *Thunnus albacares*, 21 stomachs (20 full, 1 empty)						Spotted porpoise, *Stenella attenuata*, 24 stomachs (23 full, 1 with traces)[1]					
	Volume		Number		Occurrence		Volume		Number		Occurrence	
	ml	%	No.	%	No.	%	ml	% (n=3)	No.	%	No.	%
Total	1,411	100.0	139	100.0	20	100.0	653	100.0	—	—	—	—
Fish	108	7.5	10	7.2	5	25.0	2	0.3	6	—	5	21.7
Exocoetidae	54	3.8	4	2.8	4	20.0	1	0.2	4	—	4	17.4
Oxyporhamphus micropterus	24	1.7	2	1.4	2	10.0	—	—	1	—	1	4.4
Exocoetus monocirrhus	0	—	0	—	0	—	1	—	2	—	2	8.7
Exocoetus sp.	29	2.0	1	0.7	1	5.0	—	—	0	—	0	—
Unid. exocoetid	8	0.6	1	0.7	1	—	—	—	1	—	1	4.4
Scombridae: Unid. scombrid	0	—	0	—	0	—	—	—	1	—	1	4.4
Unid. fish	54	3.7	6	4.3	2	10.0	tr.	—	2	—	2	8.7
Cephalopods	633	43.9	77	55.4	0	—	652	99.9	85	—	23	100.0
Onychoteuthidae: *Onykia* sp.	0	—	0	—	0	—	tr.	—	4	—	1	4.4
Ommastrephidae	615	42.7	38	27.3	11	55.0	650	99.5	49	—	3	100.0
Ommastrephid A (probably *Dosidicus gigas*)	609	42.3	27	19.4	10	50.0	515	78.9	35	—	3	100.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	6	0.4	11	7.9	4	20.0	135	20.7	14	—	1	33.3
Enoploteuthidae: *Abraliopsis affinis*	0	—	0	—	0	—	tr.	—	31	—	3	100.0
Unid. octopod	tr.	—	1	0.7	1	5.0	0	—	0	—	0	—
Unid. cephalopod fragments	18	1.3	—	—	1	5.0	2	0.3	—	—		33.3
Unid. cephalopod beaks	tr.	—	2	1.4	2	10.0	tr.	—	1	—	1	33.3
Crustaceans: Portunidae: *Euphylax dovii*	700	48.6	37	26.6	14	70.0	0	—	0	—	0	—

[1] Complete contents were preserved and volumed for only three stomachs. All fish remains were preserved; therefore the sample size for fish number and occurrence is 23. For cephalopod taxa, the sample size is three.

to those in Haul 2. Overlap was greatest in the cephalopod component. The crab *Euphylax dovii* was dominant in the tuna and absent in the porpoise. The enoploteuthid squid *Abraliopsis affinis* was again present in the porpoise but absent from the tuna. Nearly all of the fish volume in the tuna was due to the presence of four frigate mackerel, *Auxis* sp., in one stomach.

Haul 4

Tuna and spotted porpoise were again sampled in Haul 4 (Table 5), and the same pattern emerged as in the previous hauls. Portunid crabs were important in the tuna but absent in the porpoise, and enoploteuthid squid were present in the porpoise but absent in the tuna. Except for *Abraliopsis*, the squid and fish components were very similar for the two species in this haul.

Haul 5

Both the tuna and the spotted porpoise in this haul were engorged with freshly ingested *Auxis* and squid (Table 6), and the makeup of the contents in both volume and number was remarkably similar. They had obviously fed on the same food at the same time. *Abraliopsis*

TABLE 6.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 5.

	Yellowfin tuna, *Thunnus albacares*, 19 stomachs (all full)						Spotted porpoise, *Stenella attenuata*, 20 stomachs (17 full, 2 with traces, 1 empty)			
	Volume		Number		Occurrence		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	No.	%	No.	%
Total	17,411	100.0	222	100.0	19	100.0	194	100.0	19	100.0
Fish	13,019	74.8	110	49.6	19	100.0	[1]97	<50.0	16	84.2
Exocoetidae:										
Oxyporhamphus micropterus	197	1.1	8	3.6	6	31.6	1	<0.5	1	5.3
Exocoetus volitans	107	0.6	5	2.3	4	21.1	1	<0.5	1	5.3
Unid. exocoetid	29	0.2	1	0.5	1	5.3	0	—	0	—
	61	0.4	2	0.9	2	10.5	0	—	0	—
Scombridae: *Auxis* sp.	12,720	73.1	91	41.0	19	100.0	91	<46.9	15	79.0
Unid. fish	102	0.6	11	5.0	5	26.3	5	<2.6	5	26.3
Cephalopods	4,392	25.2	112	50.5			[2]>97	>50.0	18	94.7
Onychoteuthidae: *Onykia*	0	—	0	—	0	—	present		—	—
Ommastrephidae: Ommastrephid A (probably *Dosidicus gigas*)	4,389	25.2	88	39.6	15	79.0	present		—	—
Ommastrephid B. (probably *Symplectoteuthis* sp.)	tr.	—	10	4.5	4	21.1	present		—	—
Enoploteuthidae: *Abraliopsis affinis*	tr.	—	3	1.4	2	10.5	present		—	—
Unid. cephalopod fragments	3	<0.1	—	—	1	5.3	—		—	—
Unid. cephalopod beaks	tr.	—	11	5.0	5	26.3	—			

[1] Fish counted in 19 stomachs.
[2] Whole squid counted in 16 stomachs not saved ; only samples of beaks were saved for identification.

was present in the tuna (beaks from three individuals), the only occurrence in tuna in the six hauls. *Onykia*, however, was again present in the porpoise but not in the tuna.

Some of the frigate mackerel were sufficiently undigested to allow them to be measured. Thirty five ranged from 18 to 29 cm fork length (average 24 cm), and sizes did not differ in porpoise and tuna.

Haul 6

Nineteen stomachs of spinner porpoise were examined in this haul, and all were empty. The spotted porpoise contained freshly ingested *Auxis* and squid (Table 7), in about the same ratio as in Haul 5, but the tuna contained only small amounts of *Euphylax dovii*, along with well-digested fish and squid remains. The three species in this haul had fed on different food and/or at different times.

Summary of Results

Ommastrephid squid A (probably *Dosidicus gigas*) was the most important prey species in terms of co-occurrence in the tuna and both species of porpoise as an important food item (Table 8). The greatest overlap between species was in Haul 5, when *Auxis* and the ommastrephid were important in the tuna and the spotted porpoise. As regards specialization, *Diogenichthys* sp., *Benthosema panamense*, *Vinciguerria* sp., and *Bregmaceros* sp. were important only in the spinner porpoise, and *Euphylax dovii* was important only in the tuna. When spinner porpoise were sampled (three hauls), the rate of occurrence of empty stomachs and the state of

TABLE 7.—Stomach contents of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single net haul: Haul 6.

	Yellowfin tuna, *Thunnus albacares*, 5 stomachs (4 full, 1 empty)						Spotted porpoise, *Stenella attenuata*, 19 stomachs (12 full, 4 with traces, 3 empty)				Spinner porpoise, *S. longirostris*, 19 stomachs (all empty)
	Volume		Number		Occurrence		Number		Occurrence		
Food item	ml	%	No.	%	No.	%	No.	%	No.	%	
Total	217	100.0	>33	100.0	4	100.0	>113	100.0	16	100.0	
Fish	68	31.3	6	18.1	3	75.0	32	<28.3	9	56.3	
Exocoetidae:											
Oxyporthamphus micropterus	15	6.9	1	3.0	1	25.0	0	—	0	—	
Scombridae:											
Auxis sp.	0	—	—	—	0	—	32	<28.3	9	56.3	
Unidentified fish	53	24.4	5	<15.2	3	75.0	0	—	0	—	
Cephalopods	tr.	—	>8	>24.2	4	100.0	[1]>81	>71.7	16	100.0	
Ommastrephidae	tr.	—	5	<15.2	1	25.0			—	—	
Ommastrephid A (probably *Dosdicus gigas*)											
Unidentified cephalopod beaks	tr.	—	>3	>9.1	3	75.0			—	—	
Crustaceans:											
Portunidae:											
Euphylax dovii	149	68.7	5	<15.2	2	50.0	> 0	—	0	—	

[1] Whole squid counted in 12 full stomachs, not saved; beaks not counted or saved.

digestion of the stomach contents indicated that they had not fed at the same time as the tuna and/or the spotted porpoise.

DISCUSSION

Interpretation of the feeding habits of animals from their stomach contents is complicated by two factors. First, material from the stomachs of the primary prey may be mistaken as food items of the predator. This is especially true when, as in the present study, many stomachs contain squid, which are active piscivores in their own right. However, if we are concerned only with the general depth at which feeding takes place, it makes less difference whether the fish remains found in the gut are primary or secondary in origin. When two predators show consistent differences in the probable depth origin of their stomach contents, there are at least three alternative interpretations: the two predators feed at different depth ranges (gathering the material found directly or through some secondary predator), they feed at the same depths but at different times of the day, thus taking advantage of diurnal migration of some prey species, or they feed at the same depth with one only eating prey items that were recent predators at another depth. The first explanation seems most probable.

The other complicating factor is less easy to resolve. The depth distributions of many pelagic prey items are imperfectly known. This requires that much caution be exercised when interpreting food habits of predators from data based on rare or little-known prey.

Depth Distribution of Fish

Exocoetidae

Oxyporhamphus micropterus and species of both *Exocoetus* and *Cypselurus* are all constant inhabitants of epipelagic waters. Exocoetids were extremely common in the stomachs of tuna and *S. attenuata*. Only one exocoetid otolith was found in all 46 stomachs of *S. longirostris* examined.

Scombridae

The frigate mackerel, *Auxis* sp., is another common fish of surface waters and is of relatively large size. Its occurrence in specimen stomachs parallels that of the flyingfish, often being found in *S. attenuata* and yellowfin tuna

TABLE 8.—Summary of major identified stomach constituents of yellowfin tuna, spotted porpoise, and spinner porpoise taken from mixed-species aggregations in the eastern tropical Pacific. + = present, ● = important (≥ 10% of volume and/or numbers).

	Haul number														
	1		2			3		4		5		6		
Food item	Spotted	Spinner	Tuna	Spotted	Spinner	Tuna	Spotted	Tuna	Spotted	Tuna	Spotted	Tuna	Spotted	Spinner
FISHES:														
Oxyporhamphus micropterus	+		●	+				+	+	+	+	+		(all empty)
Auxis sp.			+	●		●				●	●		●	(all empty)
Diogenichthys sp.	+	●	(Otoliths not collected)	+	+	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(all empty)
Benthosema panamense		+	(Otoliths not collected)		●	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(all empty)
Vinciguerria sp.	+	+	(Otoliths not collected)		●	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(all empty)
Bregmaceros sp.	+	●	(Otoliths not collected)	+		(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(all empty)
SQUIDS:														
Onykis sp.	●	●		+	+								(Squids not identified)	(all empty)
Ommastrephid A (probably *Dosidicus gigus*)	●	●	●	●	●	●	●	●	●	●	●	●	(Squids not identified)	(all empty)
Ommastrephid B (probably *Symplectoteuthis* sp.)	+		+	+		●	●	+	●	+	+		(Squids not identified)	(all empty)
Abraliopsis affinis	●	●		+	+		●			+	+		(Squids not identified)	(all empty)
CRAB:														
Euphylax dovii			●			●		●				●		(all empty)

and completely absent as a food item of *S. longirostris*.

Myctophidae

At least 13 species of myctophids were identified from specimen stomachs. A majority of the genera found (*Diaphus, Diogenichthys, Ceratoscopelus, Hygophum, Myctophum, Symbolophorus, Benthosema*, and *Gonichthys*) are known to reach the surface at night during the course of vertical migrations, but most remain deep during the day. A second group consisting of *Lepidophanes, Lampanyctus, Lobianchia*, and *Triphoturus* are usually not caught in near-surface waters, even at night; their migrations probably do not take them as shallow as the first group. Myctophids were a consistent major food item of *S. longirostris* and occasionally were common in *S. attenuata*.

Gonostomatidae

Vinciguerria is a vertical migrator found below 200 m during the day, ranging up to surface waters at night. Three-fourths of the full stomachs of *S. longirostris* examined for otoliths contained gonostomatid remains. In the much larger sample of spotted porpoise stomachs, only two contained a few gonostomatid otoliths.

Stromateidae

Although some young stromateoids are often associated with floating objects, adults have large depth ranges. *Cubiceps carinatus* has been taken in a midwater trawl station in large numbers. Stromateoids appeared irregularly in the stomachs of both species of porpoise.

Melamphaidae

Melamphaes and *Scopelagadus* adults normally remain below 100 to 200 m) Ebeling, 1962; Ebeling and Weed, 1963). Melamphaid otoliths were found occasionally in large numbers in *S. longirostris* stomachs and rarely (cf. Appendix 1) in those of *S. attenuata.*

Bregmacerotidae

Although *Bregmaceros* is known to occur bathypelagically and is captured in midwater trawls, it also can be found at the surface at night (Fitch and Brownell, 1968). It occurred regularly in low frequencies in both species of porpoises; larger numbers were found in one associated group of four porpoise (*S. longirostris*).

Gempylidae, Trachipteridae

Species of both these families have been found both in surface waters and at depth. A trachipterid otolith was found in the gut of one *S. longirostris*. Gempylid remains were found in two spinner porpoise stomachs, and in one *S. attenuata* from the far-west sampling area (Appendix 1).

Paralepididae, Bathylagidae, Scopelosauridae, Evermannellidae, Opisthoproctidae

Adult members of these families are not normally found near the surface. Most museum specimens have been caught in midwater trawls. A few otoliths from species in these families were regularly found in the stomachs of *S. longirostris*. Two specimens of *S. attenuata* caught in the far-west sampling location (Appendix 1) also contained otoliths from these families, including the only records of scopelosaurids and opisthoproctids. Otoliths from many myctophids and melamphaids were also found in these specimens. The overall pattern closely parallels that seen for spinner porpoise normally (e.g., Appendix 2). This indicates that spotted porpoise are capable of shifting to a mesopelagic feeding pattern, although epipelagic feeding appears to be typical. The cause of the shift is unknown.

Shomura and Hida (1965) reported that the stomach of a Hawaiian spotted porpoise contained fish of the families Paralepididae, Alepisauridae, Gempylidae, Bramidae, and Myctophidae, as well as squids (the major component), nemertean worms, and crab larvae. The fish component was similar to that for the two westernmost specimens of eastern Pacific *S. attenuata* discussed above.

Depth Distributions of Squids

No discrete depth sampling of squids has been carried out in the area where the animals were collected. Some information, however, is available on the depth distributions of some of the families concerned from other areas.

Ommastrephidae

The most abundant squids found in the stomachs were probably *Dosidicus gigas* and *Symplectoteuthis* sp. Clarke (1966) reported that *D. gigas* and species of *Symplectoteuthis* migrate to the surface at night. *Dosidicus gigas* and *Symplectoteuthis oualaniensis* have been taken in the area by dip net at the surface under lights at night (unpublished data). In this area, the ommastrephids are the most abundant epipelagic squids.

Enoploteuthidae

The enoploteuthid squid *Abraliopsis affinis* occurred next in abundance to the ommastrephids. It is a mesopelagic species. Gibbs and Roper (1972) stated that enoploteuthids undergo diurnal vertical migrations. It appears that this species may move into or is resident within the diving ranges of the two species of porpoise, but does not occur regularly in the possibly more epipelagic range of the tuna. Another possibility, of course, is that it is fed on selectively by the porpoise and not by the tuna.

Onychoteuthidae

Onykia sp. was not found in the stomachs of *Thunnus* and has not been taken by dip net at the surface in the area. However, it was found in the stomachs of the two species of porpoise and may be a mesopelagic species. Other members of the family, *Onychoteuthis* sp. for example, are regularly taken at or near the surface at night.

SUMMARY

While there is great overlap among the diets of the two porpoises and the tuna in mixed aggregations, there is evidence of specialization in prey items, time of day at which feeding occurs, and possibly in maximum feeding depth. Although the three species are intimately associated in tight mixed groups, they do not necessarily feed on the same items at the same time in the same place. If the association is food-based, however, the epipelagic ommastrephid squids seem to be the most probable candidates for a binding common factor in this region. The apparent trophic relationships among the three species can be crudely summarized in terms of taxa and depth distribution of the major prey items (Figure 2).

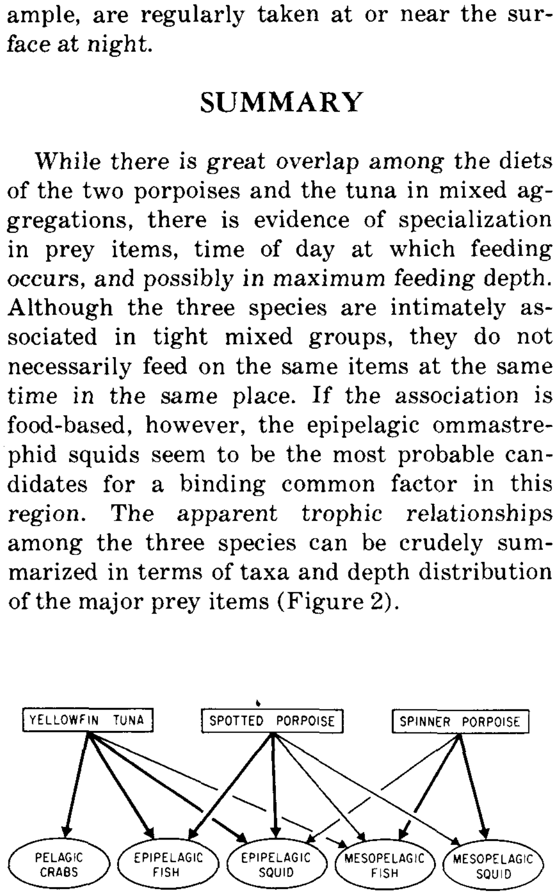

FIGURE 2.—Summary of apparent relative feeding habits of yellowfin tuna, spotted porpoise, and spinner porpoise in mixed aggregations in the eastern tropical Pacific, based on stomach-content data presented here and in Fitch and Brownell (1968) and Alverson (1963). Widths of lines crudely approximate relative importances of the major food categories.

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APPENDIX TABLE 1.—Fish identified from otoliths taken from stomachs of five spotted porpoise, *Stenella attenuata*, caught with yellowfin tuna in the eastern tropical Pacific. When more than one stomach in sample, frequency of occurrence given in parentheses. Data supplement those in Tables 2-7.

Fish	Locality			
	1	2	3	4
	7°47′N 106°50′W 18 April 1969 (1 stomach)	7°-8°N 106°-107°W 27-28 April 1969 (1 stomach)	4°-7°N 86°-100°W June-July 1970 (1 stomach)	9°28′N 129°18′W 12 Aug. 1970 (2 stomachs)
	(minimum number of individuals)			
Exocoetidae:				
Cypselurus sp.			2	
Exocoetus sp.			1	9(2)
Oxyporhamphus sp.				2(2)
Unid. exocoetid(s)	2	3		
Myctophidae:				
Diaphus spp.				34(2)
Diogenichthys laternatus				62(2)
Hygophum spp.				4(2)
Lampanyctus spp.				340(2)
Lepidophanes sp.				12(2)
Myctophum spp.				6(2)
Symbolophorus sp.				26(2)
Unid. myctophids	6		1	76(2)
Melamphaidae:				
Melamphaes spp.				18(2)
Scopelogadus sp.				29(2)
Gonostomatidae:				
Unid. gonostomatid				4(1)
Stromateidae:				
Cubiceps carinatus				9(2)
Cubiceps sp.			1	
Unid. stromateoids				5(2)
Gempylidae:				
Unid. gempylid				3(1)
Paralepididae:				
Unid. paralepidid				3(2)
Bathylagidae:				
Bathylagus sp.				23(2)
Bregmacerotidae:				
Bregmaceros sp.				2(2)
Scopelosauridae:				
Scopelosaurus sp.				1
Opisthoproctidae:				
Dolichopteryx sp.				1
Evermannellidae:				
Evermannella sp.				2(1)
Total	8	3	5	671

APPENDIX TABLE 2.—Fish identified from stomachs of 14 spinner porpoise *Stenella longirostris*, caught with yellowfin tuna in the eastern tropical Pacific. When more than one stomach in sample, frequency of occurrence given in parentheses. Data supplement those in Tables 2-7.

Fish	Locality 1	2	3	4	5	6
	7°-8°N 106°-107°W 26-27 Apr. 1969 (4 stomachs)	7°-8°N 107°W 28 Apr. 1969 (2 stomachs)	3°-10°N 110°-120°W June 1970 (1 stomach)	10°19'N 135°38'W 5 Aug. 1970 (1 stomach)	9°47'N 133°25'W 11 Aug. 1970 (5 stomachs)	9°10°N 128°-136°W Aug. 1970 (1 stomach)
Exocoetidae:						
Oxyporhamphus micropterus	1					
Myctophidae:						
Ceratoscopelus sp.	6(1)		1			1
Diaphus spp.	102(3)	3(2)	57	1	191(5)	58
Diogenichthys laternatus			624	5	3,347(5)	398
Diogenichthys sp.	8,732')3)	109(1)				
Hygophym spp.	100(1)	3(1)	4		60(5)	7
Lampanyctus parvicauda	8(3)	2(2)				
Lampanyctus idostigma	111(2)	10(1)				
Lampanyctus spp.			613	163	2,369(5)	899
Lepidophanes sp.			14		131(4)	15
Lobianchia dofleini			239		582(5)	236
Myctophum aurolaternatum	195(2)	1				
Myctophum spp.					10(3)	
Symbolophorus sp.	17(2)		12	1	38(5)	9
Benthosema panamense	68(2)	12(2)				
Gonichthys tenuiculum	79(2)					
Triphoturus sp.	3(1)					
Unid. myctophids	115(4)	29(1)			179(4)	8
Melamphaidae:						
Melamphaes spp.	6(1)	1	2		42(2)	
Scopelogadus bispinosus	1	2(1)		49		
Gonostomatidae:						
Vinciguerria sp.	32(2)	4(1)	50		55(5)	42
Unid. gonostomatids			2		52(2)	1
Stromateidae:						
Cubiceps carinatus	10(1)	1	1	6	2(2)	4
Cubiceps sp.					2(1)	
Unid. stromateoids	3(2)		3		3(2)	2
Gempylidae:						
Unid. gempylid				2	1	
Paralepididae:						
Unid. paralepidid			2			
Bathylagidae:						
Bathylagus sp.	22(1)		11		2(1)	5
Bregmacerotidae:						
Bregmaceros sp.	1		2		9(4)	1
Evermannellidae:						
Evermannella sp.	5(1)		1		2(2)	
Stomaitidae:						
Unid. stomiatoids	1		1			
Trachipteridae:						
Trachipterus fukuzakii	1					
Total	9,619	177	1,639	227	7,167	1,686

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